

## *Pholidichthys anguis*, a new species of pholidichthyid fish from Northern Territory and Western Australia

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*Abstract.*—*Pholidichthys anguis* is only the second species known in the family Pholidichthyidae. It differs from *P. leucotaenia* in having 87–98 dorsal-fin rays (vs. 66–79), 70–81 anal-fin rays (vs. 49–62), 90–101 total vertebrae (vs. 71–79), a more slender body, and a shorter head and maxillary. In addition, the color pattern of juveniles (~50–103 mm SL) differ in having the depth of the slender dark stripe on midside at vertical from anal-fin origin about 1 mm, usually much less (vs. depth 2.5–3.3 mm). Study of whole specimens and skeletal preparations of *P. anguis* indicates that the species exhibits the same familial specializations as *P. leucotaenia*. The two species are distributed allopatrically. We hypothesize that the common ancestor of the two species of *Pholidichthys* had a Tethyan distribution exclusive of Australia-New Guinea (ANG). When ANG collided with SE Asia, the ancestor invaded ANG. During a subsequent interglacial period, ecological factors contributed to the isolation of the Australian portion of the ancestral population from the New Guinea portion, and permitted divergence of the isolates.

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*Pholidichthys* and its only included species, *P. leucotaenia*, sole representative of the Pholidichthyidae, were described by Bleeker (1856) from Boeroe (= Buru), Indonesia. A purported second species, *P. anguilliformis*, was described by Lockington (1882) from the Gulf of California. The holotype of *P. anguilliformis* has not been seen since its description, but characters given for the species (especially its all spinous dorsal fin) and its type locality, probably indicate that it is not congeneric or confamilial with *Pholidichthys* Bleeker. Larson (in Trnski et al. 1989) indicated that an undescribed species of *Pholidichthys* (whose description is the main purpose of the present paper) also exists in the Indo-Pacific. Her report was based on specimens brought to her attention by prawn researchers of the Northern Territory Fisheries Division, Darwin. We know of no other de-

scribed or undescribed taxa that are referable to the Pholidichthyidae.

In the last major study of *Pholidichthys*, Springer & Freihofner (1976) reviewed the literature on *P. leucotaenia* and described aspects of its osteology, neurology, and ontogenetic color-pattern changes. They also remarked on its behavior in aquaria, plotted its geographic distribution, and discussed its possible familial interrelationships.

### Materials and Methods

Specimens of the new species are listed in the description. All but one specimen, an adult female, 245 mm SL, which we designate holotype, are small juveniles (most less than 70 mm SL, none between 103 mm and 245 mm) obtained from trawl hauls. Most of the specimens are curled and twisted and do not permit accurate SL measure-

ments to be made. We arbitrarily selected a few specimens in good condition on which to take measurements (Table 1, Fig. 6). Nevertheless a cursory examination of many specimens convinces us that the main proportional differences we stress will hold when more specimens in good condition become available for measurement.

Comparative material of *Pholidichthys leucotaenia* is that listed by Springer & Freihofner (1976:2) and more recent material or records as follows: New Caledonia (Burgess & Axelrod 1975:fig. 65, photograph; see discussion in Springer 1982:71); Solomon Islands: Marau Island (Burgess & Axelrod (1975:fig. 64, photograph). Indonesia: Flores (Kuitert 1992:4, fig. E, and J. E. Randall, pers. comm.), Saparua (USNM 210334), Tulangbesi Islands (J. E. Randall, photograph, pers. comm.); Philippines: Tawi Tawi (USNM 122340, 150828, 151178), Jolo (USNM 122339), Apo (USNM 289924), Luzon (questionable record based on aquarium dealer reports). Papua New Guinea: Madang and vicinity (AMS I.34712.007, USNM 258321), d'Entrecasteaux Islands (J. E. Randall, photograph, pers. comm.). Singapore (ZMUC P.75457, obtained from an aquarium dealer).

Dorsal-, anal-, and caudal-fin rays, vertebrae, pleural, and epineural counts were made from radiographs (and from the 3 cleared-and-stained specimens). Many more specimens were radiographed than is indicated by the numbers of specimens reported in Table 2, but because of poor ossification or fineness of structure, we were unable to obtain all counts for all specimens, and for some we were unable to make any counts. Specimens were cleared with trypsin and counterstained with alizarin and alcian blue. Dorsal- and anal-fin ray counts include all elements (last two rays counted as two—last ray not split to base). Precaudal vertebrae are those anterior vertebrae lacking a hemal spine. Measurements were made with dial calipers and recorded to three significant figures. Standard length

(SL) was taken from the midtip of the upper lip to the midbase of the caudal fin; head length (HL), from the midtip of the upper lip to the posteriormost edge of the operculum; snout length, from the midtip of the upper lip to the anteriormost edge of the orbit; upper jaw length, from the midtip of the upper lip to the posteriormost edge of the maxilla; predorsal length, from the midtip of the upper lip to the anterior base of the first dorsal-fin ray; orbital diameter is the greatest horizontal diameter; postorbital head length was taken from the posteriormost edge of the orbit to the posteriormost edge of the operculum; body depth was measured vertically at the anal-fin origin; mid-lateral dark stripe depth was measured where the stripe crossed a vertical from the anus; caudal-fin length is the length of the longest caudal-fin ray. Regression formulae and plotted curves are the products of a computer software program, PSI-Plot, version 3 (Poly Software International, P.O. Box 526368, Salt Lake City, UT 84152). Institutional abbreviations are those given by Leviton et al. (1985).

*Pholidichthys anguis*, new species

Figs. 1–3

*Holotype*.—NTM S.11799-001, mature female, 245 mm TL, WSW of Angurugu, Groote Eylandt, Northern Territory, Australia (14°05'S, 136°15'E), 19 m, 30 June 1984, Northern Territory Fisheries.

*Paratypes*.—130 specimens (~50–103 mm SL): AMS I.36375-001 (3), ANSP 173800 (3), BMNH 1995.8.14.1–3 (3), BPBM 36786 (3), CAS 82409 (3), MNHN 1995-0896-0898 (3), NTM S.13530-003 (26), QM I.30118 (3), ROM 69314 (3), USNM 337859 (9) and WAM P.31012-001 (3), all with same data: Arafura Sea, Northern Territory, North Goulburn Island (10°23'49"S, 135°43'53"E), depth 53 m, 23 Sept 1992. NTM S.13529-001 (49) and USNM 337860 (15, including 3 cleared and stained), Arafura Sea, Northern Territory, W of Cape Wessel (10°57.2'S, 136°06.2'E),

depth 42–43 m, 22 Sept 1992. NTM S-13039-001 (3), Arafura Sea, Northern Territory, N of Melville Island (10°38'S, 130°52'E), 17 June 1989. NTM S-13339-002 (1), Timor Sea, Western Australia, Joseph Bonaparte Gulf (13°07'S, 128°56'E), depth 70 m, 23 Nov 1990.

*Diagnosis*.—A species of *Pholidichthys* with: 87–98 dorsal-fin rays; 70–81 anal-fin rays; 90–101 total vertebrae; depth of slender, dark stripe on midside of juveniles (up to at least 103 mm SL) 1.0 mm or less at vertical from anal-fin origin.

*Description* (Tables 1–2).—Dorsal fin 87–98, all rays segmented, all but a few of the most anterior and posterior rays branched (unable to determine condition in holotype), anteriormost ray not supernumerary, last ray not split to base, stay (Johnson 1984:caption of table 120) present. Supraneurals or predorsal bones absent.

Anal fin 70–81 (Table 2), all rays segmented, all but a few of the most anterior and posterior rays branched (unable to determine condition in holotype), anteriormost ray apparently supernumerary (anteriormost pterygiophore appears to be fusion of two pterygiophores), last ray not split to base, stay present; 7–10, usually 8 or 9, pterygiophores anterior to first hemal spine.

Vertebrae 23–28 + 64–75 = 90–101 (Table 2); posteriormost pleural rib articulating with next- to posteriormost or posteriormost precaudal centrum; epineurals 18–22.

Pectoral-fin rays 14 or 15 (14 in 16 of 17 specimens checked), dorsal- and ventral-most two rays simple, others branched.

Pelvic-fin small, rays I,2 or I,3; spine greatly reduced, visible only in osteological preparations; third (innermost) segmented ray greatly reduced when present, usually visible only in osteological preparations; segmented rays all simple; basipterygia abutting posteriorly, widely separated anteriorly; rays supported by an almost spherical cartilaginous process at ventroposterior end of basipterygium.

Caudal-fin rays 10, all simple, 5 rays above and 5 below diastema, parhypural

and hypurals fused into single plate, no procurrent rays, no epurals.

Gillrakers on first arch (epibranchial-angle-hypobranchial; left side/right side): 5-1-8/5-1-8 (holotype); 5-1-9/5-1-8, 5-1-9/5-1-9, 6-1-9/6-1-10 (three cleared-and-stained specimens, left & right sides).

One nostril (anterior) each side; number and distribution of sensory pores as in *P. leucotaenia* (Springer & Freihofer 1976: figs. 12 and 14), except that interorbital commissural pore (Springer & Freihofer 1976:fig. 12) varying from present and obvious to absent.

Teeth: In general, all teeth are moderately laterally compressed canines with slightly recurved tips. In juveniles, ~80 mm SL, upper teeth on each side of each jaw arranged in 3 linear rows; most posterior row with smallest teeth, consisting of about 10 teeth, of which anteriormost 2 are overlapped externally by posteriormost 1 or 2 teeth of next row anterior, which consists of about 8 slightly larger teeth, of which anteriormost 2 or 3 are overlapped externally by posteriormost 2 or 3 teeth of next row anterior, which consists of about 6 teeth, which are initially larger but decrease in size and become misaligned anteriorly; external to small, misaligned teeth of previous row are largest 4 teeth. Anterior, largest teeth of upper jaw larger than those of lower jaw. In the holotype, the tooth rows have been disrupted and there appears to be 1 row of teeth posteriorly grading into 3 irregular rows anteriorly, with the outermost anterior teeth the largest.

Measurements of certain body characters are given in Table 1, and four of these characters are plotted (Fig. 6) against SL with their best fitted regression curve (usually a power curve) for comparison with the same characters in *P. leucotaenia*.

Color pattern (Figs. 1–3): All but 1 of the available specimens are juveniles of about 25 to 103 mm SL. The color pattern of the juveniles is fairly consistent, but the dark markings we describe vary from faintly to darkly dusky, and may be interrupted. We

Table 1.—Measurements in millimeters (and as percent SL) for certain characters of the species of *Pholidichthys*.

	<i>P. anguis</i>						
SL	69.1 <sup>1</sup>	76.7 <sup>1</sup>	77.3 <sup>2</sup>	86.0 <sup>1</sup>	87.4 <sup>2</sup>	103 <sup>2</sup>	245 <sup>3</sup>
Head length	11.7 (16.9)	12.1 (15.8)	12.1 (15.7)	13.5 (15.7)	13.6 (15.6)	14.6 (14.2)	22.2 (9.1)
Snout length	2.2 (3.2)	2.4 (3.1)	2.4 (3.1)	2.8 (3.3)	2.8 (3.2)	3.0 (2.9)	4.5 (1.8)
Orbital diameter	3.1 (4.5)	2.5 (3.3)	3.2 (4.1)	3.0 (3.5)	3.4 (3.9)	3.2 (3.1)	3.4 (1.4)
Postorbital HL	6.9 (10.0)	7.6 (9.9)	7.1 (9.2)	8.2 (9.5)	8.6 (9.8)	9.0 (8.7)	15.2 (6.2)
Upper jaw length	4.3 (6.2)	4.1 (5.3)	4.3 (5.6)	4.6 (5.4)	4.7 (5.4)	5.3 (5.1)	7.6 (3.1)
Predorsal length	11.9 (17.2)	12.5 (16.3)	12.4 (16.1)	13.4 (15.6)	13.1 (15.0)	14.2 (13.7)	25.1 (10.2)
Body depth	4.7 (6.8)	5.0 (6.5)	5.5 (7.1)	5.9 (6.9)	6.0 (6.9)	6.3 (6.1)	10.3 (4.2)
Caudal-fin length	5.1 (7.4)	5.1 (6.6)	5.2 (6.7)	5.6 (6.5)	5.5 (6.3)	7.0 (6.8)	14.5 (5.9)
Mid-lateral dark stripe depth	0.6 (0.9)	0.7 (0.9)	0.5 (0.6)	0.9 (1.0)	1.0 (1.1)	0.9 (0.9)	NA
	<i>P. leucotaenia</i>						
SL	49.7 <sup>4</sup>	52.1 <sup>5</sup>	66.2 <sup>4</sup>	77.6 <sup>5</sup>	79.4 <sup>5</sup>	80.2 <sup>6</sup>	83.3 <sup>6</sup>
Head length	10.0 (20.1)	11.6 (22.3)	13.0 (21.2)	15.1 (19.5)	15.4 (19.4)	16.6 (20.7)	16.4 (19.7)
Snout length	2.2 (4.4)	2.5 (4.8)	2.4 (3.9)	3.2 (4.1)	3.4 (4.3)	3.4 (4.2)	3.5 (4.2)
Orbital diameter	2.5 (5.0)	3.0 (5.8)	2.8 (4.6)	3.0 (3.9)	3.2 (4.0)	3.2 (4.0)	3.1 (3.7)
Postorbital HL	6.8 (13.7)	7.0 (13.5)	8.2 (20.8)	9.4 (12.1)	10.1 (12.7)	10.2 (12.7)	10.6 (12.7)
Upper jaw length	3.2 (6.4)	3.8 (7.3)	4.2 (6.8)	5.2 (6.7)	5.0 (6.3)	5.3 (6.6)	5.2 (6.2)
Predorsal length	11.8 (23.8)	10.7 (20.5)	13.4 (21.9)	14.7 (18.9)	15.3 (19.3)	15.8 (19.7)	15.5 (18.6)
Body depth	5.2 (10.4)	4.6 (8.8)	6.3 (9.5)	6.7 (8.6)	7.1 (8.9)	8.8 (11.0)	9.3 (11.2)
Caudal-fin length	4.2 (8.4)	4.4 (8.4)	4.3 (7.0)	—	—	5.7 (7.1)	6.9 (8.3)
Mid-lateral dark stripe depth	3.0 (6.0)	2.5 (4.8)	3.3 (5.4)	3.3 (4.3)	2.8 (3.6)	2.7 (3.4)	2.7 (3.2)
	<i>P. leucotaenia</i>						
SL	97.5 <sup>7</sup>	102 <sup>8</sup>	115 <sup>9</sup>	224 <sup>10</sup>	225 <sup>10</sup>	337 <sup>11</sup>	
Head length	17.3 (17.8)	18.9 (18.5)	20.3 (17.6)	30.5 (13.6)	28.7 (12.8)	41.8 (12.4)	
Snout length	3.5 (3.6)	3.6 (3.5)	4.0 (3.5)	6.3 (2.8)	6.5 (2.9)	7.8 (2.3)	
Orbital diameter	3.5 (3.6)	3.5 (3.4)	3.6 (3.1)	5.2 (2.3)	4.6 (2.0)	5.2 (1.5)	
Postorbital HL	10.8 (11.1)	12.0 (11.8)	13.3 (11.6)	20.5 (9.2)	19.2 (8.5)	31.0 (9.2)	
Upper jaw length	6.0 (6.2)	6.0 (5.9)	6.6 (5.7)	10.9 (4.9)	10.6 (4.7)	14.1 (4.2)	
Predorsal length	17.2 (17.6)	18.2 (17.8)	18.7 (16.3)	30.1 (13.4)	27.8 (12.4)	42.7 (12.7)	
Body depth	8.5 (8.7)	7.6 (7.4)	8.9 (7.7)	19.4 (8.7)	18.1 (8.0)	20.7 (6.1)	
Caudal-fin length	6.5 (6.7)	7.7 (7.5)	8.9 (7.7)	14.2 (6.3)	14.4 (6.4)	—	
Mid-lateral dark stripe depth	3.3 (3.4)	2.8 (2.7)	3.1 (2.7)	NA	NA	NA	

<sup>1</sup>USNM 337860, <sup>2</sup>NTM S.13039-001, <sup>3</sup>Holotype, NTM S.11779-001; <sup>4</sup>AMS I.34480-001, <sup>5</sup>USNM 289924, <sup>6</sup>USNM 215258, <sup>7</sup>AMS I.34712-007, <sup>8</sup>USNM 122340, <sup>9</sup>USNM 150828, <sup>10</sup>CAS 32048, <sup>11</sup>USNM 212163.

describe the dark markings in their most pronounced and complete form. Tip of chin with dark smudge, another on snout above upper lip continuing ventrally below eye and posteriorly from mid-postorbital margin as broad, dark stripe; stripe constricting at upper posterior margin of operculum and continuing as dark, slender midlateral stripe, which decreases in depth (depth at no point much greater than 1 mm, usually less) as it proceeds posteriorly to base of caudal fin, where it is briefly interrupted, beginning

again, slightly intensified, on caudal fin, and extending, diffusely, for variable distance, up to the end of the fin. Slender, dark stripe dorsally on head, originating at postorbital margin, continuing posteriorly just ventral to dorsal-fin base, tapering and becoming fainter posteriorly until it vanishes, usually on or before reaching posterior third of body. No other prominent markings on head, body, or fins.

Female adult (holotype, 245 mm SL). Head overall dusky with darker, diffuse

Table 2.—Frequency distributions for certain meristic characters of the species of *Pholidichthys* (localities arranged west to east). “x” denotes count recorded by Kailola (1973:11), but not encountered during our study. ? denotes a specimen with a count equal to or slightly greater than indicated by the column heading.

		Dorsal-fin rays																																			
Species		66	67	68	69	70	71	72	73	74	75	76	77	78	79	...	86	87	88	89	90	91	92	93	94	95	96	97	98								
<i>P. anguis</i>																																					
	J. Bonaparte Gulf																																				
	N Melville Id																																				
	N. Goulburn Id																																				
	Cape Wessel																																				
	Groote Eylandt																																				
<i>P. leucotaenia</i>		x	x	x	x	x	x	3	3	1	1	8	4	1	1																						
		Anal-fin rays																																			
Species		49	50	51	52	53	54	55	56	57	58	59	60	61	62	...	70	71	72	73	74	75	76	77	78	79	80	81									
<i>P. anguis</i>																																					
	J. Bonaparte Gulf																																				
	N Melville Id																																				
	N. Goulburn Id																																				
	Cape Wessel																																				
	Groote Eylandt																																				
<i>P. leucotaenia</i>		x	x	x	x	x	2	1	-	4	4	3	1	6	1																						
		Total vertebrae																																			
Species		71	72	73	74	75	76	77	78	79	...	90	91	92	93	94	95	96	97	98	99	100	101														
<i>P. anguis</i>																																					
	J. Bonaparte Gulf																																				
	N. Melville Id																																				
	N. Goulburn Id																																				
	Cape Wessel																																				
	Groote Eylandt																																				
<i>P. leucotaenia</i>		1	-	2	4	3	2	5	6	1																											
		Precaudal vertebrae										Caudal vertebrae																									
Species		22	23	24	25	26	27	28	48	49	50	51	52	53	54	55	56	...	64	65	66	67	68	69	70	71	72	73	74	75							
<i>P. anguis</i>																																					
	J. Bonaparte Gulf																																				
	N. Melville Id																																				
	N. Goulburn Id																																				
	Cape Wessel																																				
	Groote Eylandt																																				
<i>P. leucotaenia</i>		2	4	9	11	1	2	1	7	2	3	5	3	1	1																						

<sup>1</sup>Specimen has caudal vertebral fusions, which may have affected number of fin rays; caudal and total vertebral counts for this specimen not included in table.

dusky blotch posterior to orbit; blotch interrupted at preopercular margin, becoming much less distinct on opercle, continuing on body as moderately large, indistinct series of ovoid to elongate ovoid dusky areas, which become unrecognizable at about body midlength. Three horizontal pairs of dusky ovoid spots on abdomen (anteriorly,

at midlength, posteriorly) continuing as series of about 20 diffuse, dusky spots on body below midlevel, spots ending on posterior half of body. Series of diffuse ovoid spots on dorsal body contour, beginning over posterior quarter of abdomen, continuing to caudal-fin.

Dorsal and anal fins variably dusky, with

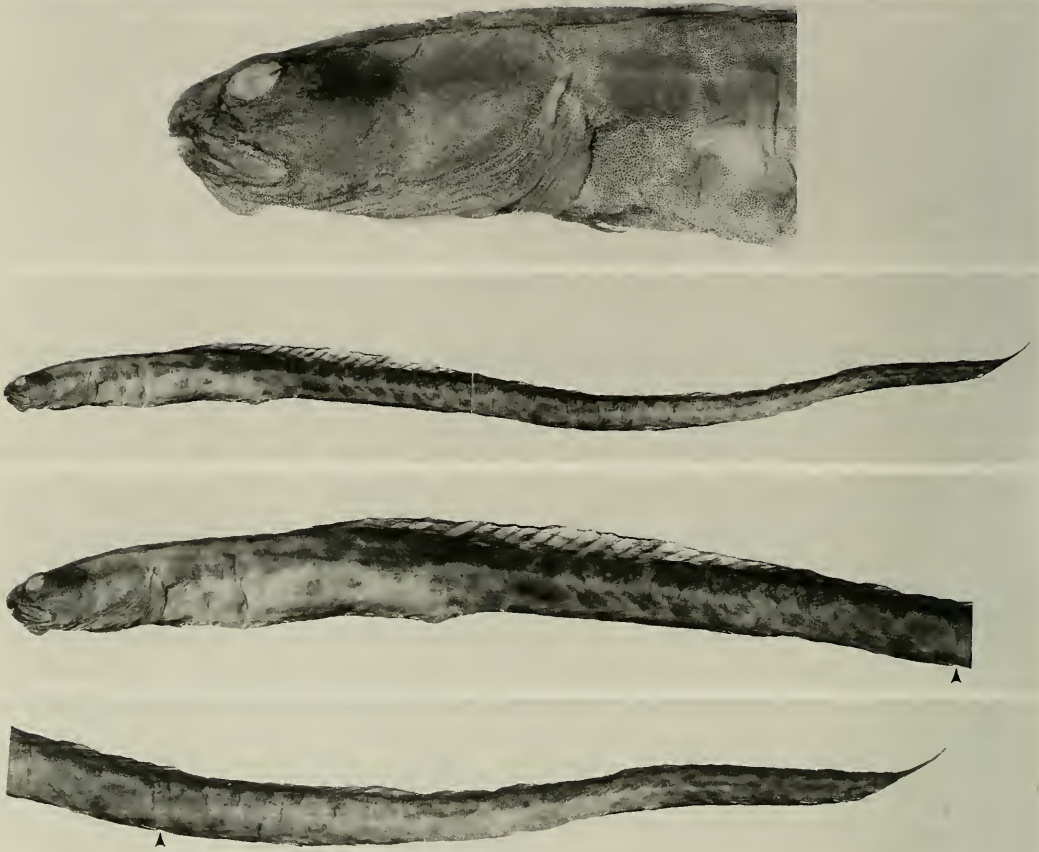


Fig. 1. Holotype of *Pholidichthys anguis*, NTM S.11799-001, female 245, mm SL, WSW of Groote Eylandt, Gulf of Carpentaria, Northern Territory, Australia. Bulge under lower jaw appears to be an abnormality. Full-length view is produced from two photographs pieced together. Arrows in lower two figures indicate same position in each photograph. (Photographs by T. B. Griswold)

distal edge of each darker; both fins becoming much darker near posterior end, where they join darkly dusky caudal fin. Pectoral and pelvic fins pale dusky. A color photograph taken of the fresh specimen shows the spots on the body to be brownish; background color tan. Large yellow eggs are visible through the transparent abdomen.

*Remarks.*—The holotype has an apparently abnormal padlike swelling on the chin, possibly caused by a parasite. As seen through the body wall of the holotype (Fig. 2), the maximum diameter of the eggs appears to be approximately 2 mm.

All specimens of *P. anguis* have come

from benthic trawl samples from a mud substrate, which may include sand, shell, sponges, and rocky reef and coral patches. None have been found associated with coral reefs, as with *P. leucotaenia*.

*Comparisons.*—Study of whole specimens and skeletal preparations of *P. anguis* indicates that the species exhibits the same familial specializations as *P. leucotaenia* (e.g., presence of a septal bone, fused 5th ceratobranchials, single nostril, no spinous fin rays, lack of scales, etc; see Springer & Freihofner 1976). *Pholidichthys anguis* differs from *P. leucotaenia* in having 87–98 dorsal-fin rays (vs. 66–79), 70–81 anal-fin



Fig. 2. Holotype of *Pholidichthys anguis*, NTM S.11799-001, from color photograph taken when specimen was freshly collected; note eggs visible through transparent abdominal skin. (Photograph by A. Baker)

rays (vs. 49–62), 90–101 total vertebrae (vs. 71–79), a more slender body, shorter head, predorsal, and upper jaw lengths, lesser body depth (Fig. 6), and in the color pattern of juveniles, ~50–103 mm SL (depth of slender dark stripe on midside at vertical from anal-fin origin up to about 1 mm, usually much less, as opposed to depth 2.5–3.3 mm in *P. leucotaenia*; Table 1; also compare Figs. 3 and 4). The adult color pattern, apparently, is also different from that of *P. leucotaenia* (Fig. 5), although appearing somewhat similar to that of the preadult (Figure 5, middle). Only one adult of *P. anguis* is known, and it is conceivable that the pattern is as variable as that of *P. leucotaenia*. Interestingly, adults of *P. leucotaenia* are known only from aquarium raised juveniles, and none have been seen in the wild or collected.

*Etymology.*—The specific name is from the Latin *anguis*, meaning “snake,” refers to the elongate form of the species, and is here used as a noun in apposition.

#### Distribution and Historical Biogeography

*Pholidichthys anguis* is known only from the coastal waters of Northern Territory between 128°56' and 136°15'E in depths of 19–70 m (Fig. 7). Its distribution is allopatric to that of *P. leucotaenia*, which is known from habitats close to or among corals, from the southern Philippines south to Flores, Indonesia, and east and south to New Caledonia. We question two other locality records. Specimens indicated as originating from Calatagan, Batangas [Province], Luzon, Philippines (CAS 32048, 76415), were provided by aquarium importers, as seems to be the case with a specimen purportedly from Batangas (BMNH 1982.8.3.4). A Batangas locality appears to be reasonable, but should be verified by better documented new collections. To explain the current distributions of these two species, we propose the following scenario:

Wilson & Allen (1987:64) concluded that “the pan-tropical Tethyan fauna and its successor, the modern Indo-West Pacific

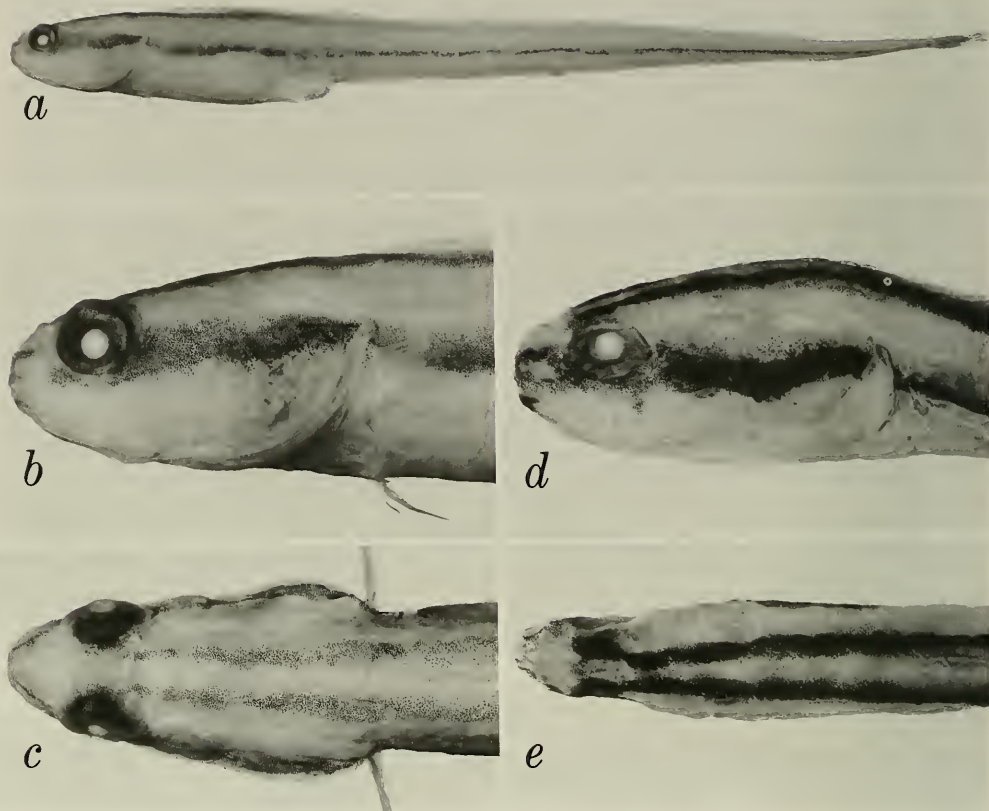


Fig. 3. *Pholidichthys anguis*, juveniles, Northern Territory, Australia. *a-c*, NTM 13039-001, 87.8 mm SL, N of Melville Island, Arafura Sea, dusky markings relatively typical, *c* shows dorsal surface of head and anteriormost portion of body; *d-e*, NTM S.13339-002, ca. 85, mm SL, Joseph Bonaparte Gulf, dusky markings unusually intense, *e* shows dorsal surface of head and anteriormost portion of body. (Photographs by T. B. Griswold)

fauna, have dominated the northern coast of Australia since the beginning of the Tertiary [ca. 65 m.y.a.].” We believe their conclusion reasonable and hypothesize that the distribution of the common ancestor of the two species of *Pholidichthys* originated as part of the Tethyan fauna and occupied an area that excluded Australia-New Guinea. The ancestral distribution was possibly limited to the coastal areas of southeastern Asia (Malaya, Indonesia, Philippines) until, perhaps, as recently as mid-Miocene (ca. 16 m.y.a.), when southeast Asia and northern Australia-New Guinea were still separated by an expanse of deep, open sea. This expanse of sea acted as a barrier to

dispersal between the two areas, particularly for shallow-dwelling marine organisms such as *Pholidichthys*, which lacks a planktonic stage (Trnski et al. 1989, Wirtz 1991). After Australia-New Guinea collided with the islands (Banda Arc) off southeast Asia (ca. 15 m.y.a.; Audley-Charles 1981, 1987, Burrett et al. 1991), the spacing of existing and newly formed islands may have permitted shallow-dwelling organisms to disperse between the colliding entities. If so, the common ancestor of the two extant *Pholidichthys* species was then able to disperse first to northern Australia-New Guinea and then into the New Britain-New Ireland-Solomon volcanic islands





Fig. 4. *Pholidichthys leucotaenia* juveniles (ca. 60 mm SL) photographed in aquarium (R. B. Hansen).

chain. This chain originated along a mid-Pacific plate ridge during late Eocene–early Oligocene and was gradually displaced westward to converge with New Guinea during the past half million years (Kroenke 1984, Yan & Kroenke 1993). After reach-

ing the Solomons, *Pholidichthys* presumably dispersed south along the contiguous New Hebrides island chain (from which few fish collections have been made and *Pholidichthys* is as yet unreported) to close-by New Caledonia, and presumably

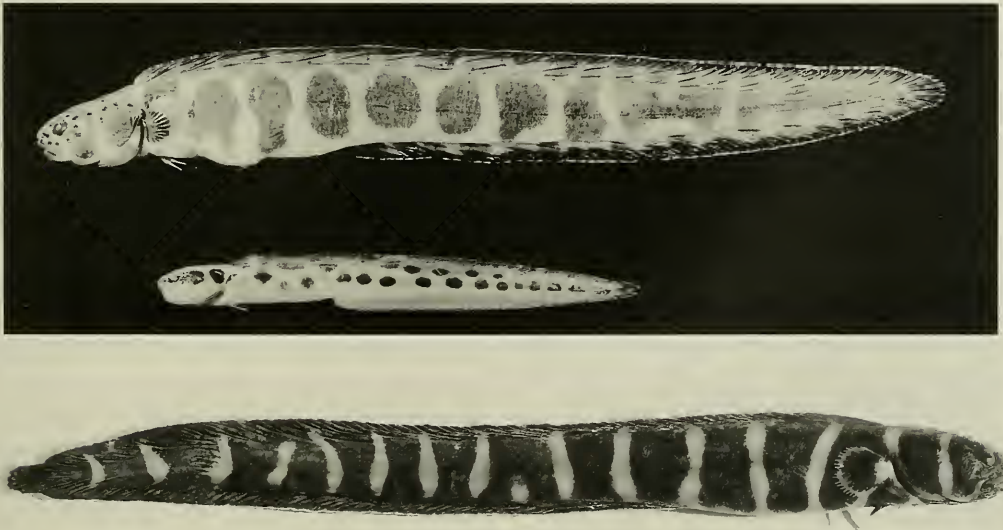


Fig. 5. *Pholidichthys leucotaenia*, aquarium specimens. Upper, adult, 205 mm SL, and middle, preadult, 108 mm, purportedly originating from Philippines (from Springer & Freihofer 1976: fig. 23); bottom, ZMUC P:75457, adult, ca. 175 mm SL, obtained from dealer in Singapore (G. Brovad, photographer).

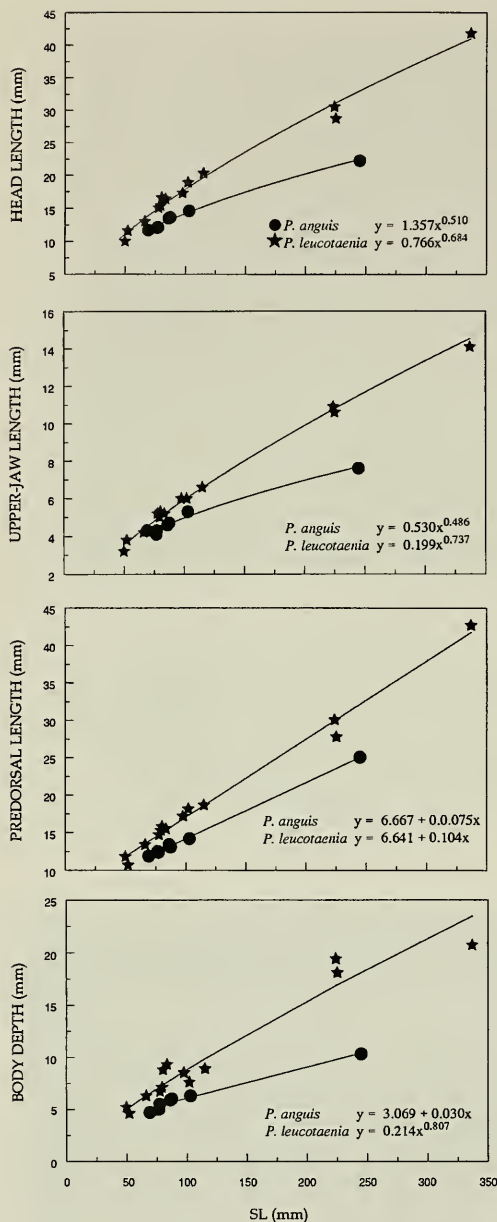


Fig. 6. Scatter plots, best-fit curves, and regression formulae for certain mensurable characters in *Pholidichthys* species based on data listed in Table 1.

the Loyalty Islands, with which the New Hebrides is colliding.

The apparent absence of *Pholidichthys* from the Queensland coast and adjacent Great Barrier Reef, where one might expect it to occur, appears puzzling at first, but

many marine forms appear to have been unable to reach these areas from New Guinea, and vice-versa (a few didactic examples: the blennioid fishes *Ecsenius namiyei*, *E. selifer*, *E. taeniatus*, *E. trilineatus* all occur in easternmost New Guinea, but are absent from the GBR; *E. mandibularis*, *E. australianus*, *E. stictus* all occur at the northern Queensland end of the GBR, but are absent from New Guinea—Springer (1988)). Coral reefs extend around the southeast tip of New Guinea and continue westward along its southern coast to about Port Moresby on the eastern side of the Gulf of Papua. The distribution of *P. leucotaenia* (Fig. 7) follows this reefal distribution. A large number of rivers drain into the western Gulf of Papua, which decreases salinity and increases turbidity in this portion of the Gulf, thus, creating a barrier to westward dispersal of many marine forms that have reached the eastern portion of the Gulf. The most apparent (shortest) dispersal route to the Great Barrier Reef from New Guinea would be down the islands and reefs that extend north from the Cape York Peninsula. This route would be blocked to the north, however, by the riverine barrier in the western portion of the Gulf of Papua, which we believe explains the absence of *Pholidichthys* and many other apparently stenohaline forms from the Great Barrier Reef and Queensland. *Pholidichthys* is present in the western Gulf of Carpentaria, where small coral reefs are also present, but not in the eastern Gulf, where no reefs are present. Heavy river drainage and sediment deposition in the eastern Gulf of Carpentaria probably also prevents the eastward dispersal of reef obligates, such as *Pholidichthys*, around the coast of the Gulf of Carpentaria to eastern Queensland and the Great Barrier Reef (Wells 1957:pl. 9, charts the world distribution of coral reefs).

The possibility of *Pholidichthys*' reaching Australia across the Arafura and Timor seas by dispersing along the southwestern coast of New Guinea and/or southeastern Indonesian island chain (Lesser Sunda to



Fig. 7. Distribution of the species of *Pholidichthys*. Solid dots—*P. leucotaenia*; triangles—*P. anguis*; C = Gulf of Carpentaria; P = Gulf of Papua; shaded area represents emergent land joining northern Australia and New Guinea during most recent glacial sea-level low, ca. 18,000 B.P. (other emergent land areas not shown).

Aru islands) would also present problems under present-day land-sea distributions. The southwestern coast of New Guinea bears numerous rivers draining into the Arafura sea and, consequently, the obligate coral-reef stepping stones are absent in the area. The present-day, relatively wide, coral-reefless expanse of the Timor and Arafura seas and the deep ocean paralleling and separating the southeastern islands from Australia are barrier enough to prevent the dispersal of forms such as *Pholidichthys*. Similarly, the barrier maintains the present-day allopatry of the two *Pholidichthys* species.

During periods of Pleistocene glaciation (latest about 18,000 B.P.), the seaway passage (Torres Strait) between central Northern Territory and southern New Guinea was closed by a broad landbridge that extended between Northern Territory and much of southern New Guinea (Myers 1989:fig. 8, Springer & Williams 1990:fig. 7). The clo-

sure of the passage probably would not have altered river flow into the western Gulf of Papua, but the emergent land would have eliminated ancestral *Pholidichthys* in the region from the Gulf of Carpentaria to somewhat west of Melville Island, ca. 130°E. The present occurrence of *Pholidichthys* (*P. anguis*) in this relatively recently re-inundated area is the result of recent dispersal into Australian coastal habitats to the west. (Springer & Williams 1994: 128, attribute east-west differences in the morphology of the blennioid *Istiblennius meleagris*, which is restricted to the northern coast of Australia, to the barrier created by formerly emergent land in the Gulf of Carpentaria-Melville Island region). We suggest that reef habitats formed along the western side of the Pleistocene landbridge that permitted dispersal of the ancestral species of *Pholidichthys* to northwestern Australia. As sea level rose and created modern conditions, the Australian and southeast

Asian populations became isolated and diverged. We are uncertain how, or if it is necessary, to accommodate for river runoff from the emergent west side of the land-bridge. Changes in the positions of river mouths on the west side would have been more radical than changes on the east side because of the greater area affected. Although we have chosen to base the final scene of our scenario on Pleistocene events of the past 18,000 years, a similar scenario could be developed for any of the earlier interglacials of the Quarternary. If only a small sample of the common ancestor reached Northern Territory and became isolated, rapid evolution (divergence) might be expected, as well as the current, apparently highly limited distribution of *P. anguis*.

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